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The Evolution of Assimilating Tissue in Sporophytes.

By Carlton C. Curtis.

In *Harper's Magazine* for November appears an article by Dr. H. S. Williams on the "Century's Progress in Biology." The author very justly ascribes an important place to the poet Goethe, whose treatise on the metamorphosis of plants, however fanciful the dream, it must be admitted, suggested lines of investigation which have yielded such important results in every department of botany, originating the study of the history of development and paving the way for the spread of the idea of the transmutation of species. The absurd speculations of the philosophy of Goethe and of his time have passed away; still his doctrine of leaf metamorphosis, though not originating with him more than with Cesalpino and Linnaeus, has been generally accepted. Goethe's ideal or typical plant with its six stages of development, cotyledon, leaf, sepal, petal, stamen and corolla, appearing in three wave crests or expansions, (leaf, petal and carpel), and three wave troughs or contractions (cotyledon, sepal and stamen) has had in the popular mind something more substantial in its conception than the stuff of which dreams are made. At the present time these organs are quite generally regarded as due to the gradual metamorphosis in acropetal succession of parts which are identical in origin; and, though not ascribing the change to the clarification and refinement of the ascending sap, we have come to look upon the metamorphosis as a progressive one from primordial leaf to carpel. As a matter of fact, however, there is probably no evidence of the metamorphosis of a leaf into any member of the flower, especially into one of the essential parts. The evolution of plant types points to an entirely distinct origin of the organs of assimilation and propagation and indicates very clearly the priority of the latter in point of time. Among lower forms, as the Algae, when an alternation can be traced, there is no indication of assimilatory tissue in the sporophyte, it being simply a sporangium. This is essentially true of the lower Hepaticae, as in *Riccia*, the fertilized egg of the archegonium is developed as a sporangium surrounded by a single layer of non-propagative cells. In the higher members of this group a more considerable sterilization of tissue is apparent in the formation of elaters and a rudimentary seta. This differentiation is carried further in the sporogonia of the Jungermaniales, and among the Anthocerotales a most suggestive distribution of labor is manifest in the differentiation of the sterile cells. The central cell mass is no longer propagative and supports a mere bell-shaped zone of archesporial tissue which is associated with assimilatory cells; the foot has developed root-like processes for the absorption of nutriment from the gametophyte, and among some forms it is especially noteworthy that certain parts of the archesporial tissue becomes sterile, separating the sporogenous tissue into irregular chambers. These features are worthy of especial consideration, for in them are seen the rudiments of the segmentations and differentiations of the higher plants. It will be seen that the entire sporogenous tissue has been advanced to near the surface of the sporogonium as a more advantageous position for the distribution of spores and an assimilatory tissue has been evolved to meet the demands made upon the plant by its ever-increasing spore production, as it advances in the biological series, and finally organs for the absorption of food, both liquid and gaseous, have been added. Thus we have a rudimentary sporophytic plant, still parasitic to be sure, but possessing three distinct functions, progagation, assimilation and absorption, and from some such type there is indication of the evolution of the higher plants.

The Musci are remotely connected with this ancestral form and show few departures, save in the gradual sterilization of the upper portion of the archesporium, but in passing to the Pteridophyta, we are confronted by a greater gap than appears between any of the other subkingdoms. So extensive has been the obliteration of the progenitors of this division in the evolutionary series, that not only is the ancestry in doubt, but the alliances of the three surviving classes themselves must remain an uncertainty. However, the lines along which the evolution took place, as well as the origin of new features, are generally manifest. The significant features of the Pteridophyta are the finally complete separation of the two generations, the separation of the sporogenous tissue into isolated portions (sporangia) and the development of appendages, lateral organs, from the sporophyte. This has been made possible through the differentiation of tissue that accompanied the perpetuation of the physiological distribution of labor noted above. The sporophyte has become a self-supporting plant, save in its embryological condition, through the perfection of its absorbtive parts and also through the formation of appendages to which are confined almost entirely the assimilatory function. These appendages, the leaves, doubtless came about in some of the classes through their ceasing to function as organs of propagation, but retaining the function of assimilation, and in other cases they may quite as reasonably be supposed to represent outgrowths of the assimilatory tissue of the sporogonial prototype. This increase of the vegetative system of the sporophyte, which renders the approach to the Pteridophyta so striking, has become a necessity since now the food absorbed is no longer organized, and more especially in order to mature the spore, the production of which reaches its culmination in this group. The stages in this evolution of the extant Pteridophyta have been hopelessly lost, but each of the subclasses presents features that suggest an anthocerotal progenitor. This relationship appears very manifest among some of the simpler of the eusporangiate Filicinae. In this primitive group appear several strong ancestral characters, and among the more significant, as appertaining to this subject, may be mentioned the structure of the so-called fertile leaf. Here is found a superficial archesporium, made septate by the sterilization of its tissue, and associated are assimilating cells and stomata—practically the duplicate of the sporogonium of *Notothylas* and *Anthoceros*. The assimilatory portion cannot longer for lack of room be confined to the propagative organ, and is developed from it, forming an appendage, the leaf, just as the root has taken on new characters. Through forms like *Botrychium*, *Danaea* and *Angiopteris* is presented a series of changes which are suggestive of the changes which led the way to the gradual separation of the sporogenous tissue into separate portions, sporangia, and their distribution over the surface of the leaf. Thus in *Anthoceros* the sporogenous tissue is imperfectly separated forming a synangium, in *Botrychium* this septation of the propagative cells is carried further by the growth of the fertile branch into a paniculate cluster of lateral appendages, in *Danaea* this expansion assumes a leaf form with the synangia covering its entire under surface and in *Angiopteris* we see the separation of the synangia into soral groups of sporangia. In the entire class of Filicinae the complete separation of the sporogenous and assimilatory function does not seem to be perfected, and in many of those species, where the propagative tissue is confined to special leaves, the ease with which they may, in many cases, be transformed to organs of assimilation would seem to indicate the transmission of an inherited tendency towards the association of these two functions.

The Equisetinae and Lycopodinae show only the remotest alliance with the Filicinae. In the former class the separation of the sporogenous and assimilation tissues has become complete, and this is true to a large degree among the Lycopods. In both groups the aggregation of the archesporial tissue about a sterile tissue, as shown in the fertile spike, is suggestive of the apical portion of a sporogonium and the development of organs to bear the sporangia recalls the trend of morphological variation, noted among the Filicinae.

This separation of function reappears essentially unaltered among the Gymnospermae and Angiospermae and the distribution of labor has now become so thoroughly relegated to certain organs as to allow the leaves a wider range of morphological variation than was possible when associated with the propagative function when the tendency to variation might have so seriously interfered with the propagative function as to have jeopardized the perpetuation of the species. The ancestral characters are still preserved in the cone and spike with their prolific spore formation, but with the advantages accruing from the aggregating of the staminate and carpellary sporophyls on a single axis as well as from the wide range of morphological variation that appertained to both the leaf and sporophyl there appears a conspicuous reduction of sporogenous tissue in approaching the highest order. Whatever view may be held as to the development of the leaf from the sporogonium, certainly it must be admitted that the sporophyls have not resulted from a metamorphosis of leaves and that essentially the reverse process has attended the evolution of plant forms. Regarding the relation of the perianth to the other appendages the ready metamorphosis of the stamens of the Rosaceae, Nympheaceae and Ranunculaceae to petaloid structures present interesting examples that indicate that the corolla, at least, may have resulted rom the sterilization of sporogenous tissue, and this seems the more probable when we associate the reduction of the essential organs of the flower with the advent of the perianth. The question may properly be asked to what category do the assimilatory appendages of the mosses belong. Physiologically they are leaves and their origin, though on an antithetic generation, is doubtless due to eruptions of the shoot brought about possibly, in some cases, through food accumulations which become a hereditary character in some plants and a fruitful source of variation, and especially has the stimulus of light been a potent factor in the development of assimilatory organs. As indicated above, a similar cause may have given rise to the leaf of the vascular plants, as is possibly true among the Filicinae, but the reduced leaf character of the Equisetinae and Lycopodinae, together with the abortion of the sporangia, certainly suggests their derivation from sterilized sporophyls. Schwendener's conception of a leaf as a lateral appendage of the shoot that differs from it in character rather than grade or rank is an excellent definition, but the failure to regard the homologies and phylogeny of these lateral organs has led to the serious misconceptions regarding morphologies so commonly recurring in text-books of botany.